Physiological adjustment to heat in Blue Tit Parus caeruleus nestlings from a Mediterranean habitat

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PHYSIOLOGICAL ADJUSTMENT TO HEAT IN BLUE TIT *PARUS CAERULEUS* NESTLINGS FROM A MEDITERRANEAN HABITAT

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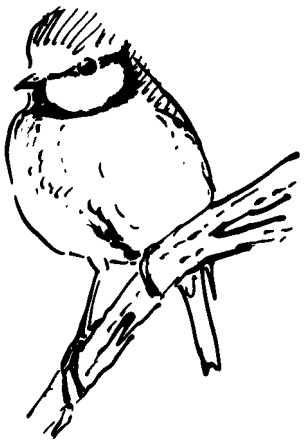
On Corsica Blue Tits *Parus caeruleus ogliastrae* breed late in the spring when ambient temperatures are high as a local adaptation to the late occurrence of their food. This means that Blue Tits rear their young when water demand of nestlings for evaporative cooling is high due to elevated temperatures, but the water content of the diet is low. Thus, the local environment may impose a water limitation on breeding tits. We therefore expected physiological adjustments in Blue Tit nestlings to a hot climate with a low availability of water, such as a reduced metabolic rate. We measured oxygen consumption and evaporative water loss of 20 full-grown nestling Blue Tits from Corsica in an open-flow respirometry system. Metabolic rate at thermoneutrality was only 0.117 W, significantly lower than expected from allometric relationships. Observed evaporative water loss at 25°C was 40.8% lower than predicted on the basis of body mass. The observed savings in evaporative water loss corresponded to the expected savings due to a reduced metabolic heat production. Thus, Blue Tit nestlings on Corsica are more similar in their physiological characteristics to species from hot and dry environments than to continental European Paridae.



Key words: *Parus caeruleus ogliastrae* - Corsica - breeding - water demand - metabolic rate - nestlings - evaporative water loss

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INTRODUCTION

A large variation in breeding parameters, such as laying date and clutch size, has been observed among different Blue Tit *Parus caeruleus* populations in the Mediterranean region where the birds breed in a complex mosaic of habitats of different quality (Blondel *et al.* 1987, 1992a, 1993; Blondel & Dias 1994). In this region tits have been studied in two distinct breeding habitats. They either breed in deciduous habitats dominated by Downy Oak *Quercus pubescens* or in a sclerophyllous habitat dominated by Holm Oak *Q. ilex*. The timing of the birds' breeding season and the number of young they can rear depend on the amount of resources available, particularly food (e.g. Lack 1968; Martin 1987; Nager & Van Noordwijk 1995). For tits feeding nestlings, the most important prey are caterpillars (Perrins 1979; Blondel *et al.* 1991; Banbura *et al.* 1994). Both the timing and the abundance of caterpillars differ between the two habitats: caterpillars in the deciduous habitat are more abundant and are most plentiful about 3 weeks earlier than in the sclerophyllous habitat (Blondel *et al.* 1987, 1993; Zandt *et al.* 1990; Blondel & Dias 1994). On Corsica sclerophyllous habitat dominates and Corsican Blue Tits of the subspecies *P.c. ogliastrae* are assumed to be geneti-

cally isolated from mainland populations (Martin & Bellot 1990). This subspecies is ca. 15% smaller than Blue Tits from the European mainland (Blondel *et al.* 1992b). In Corsican sclerophyllous habitat, tits only start to breed in early May (Blondel 1985; Blondel *et al.* 1993) thus tracking the late availability of food. Clutch size on Corsica is strongly reduced (6.5 eggs) compared to clutch sizes of 8.5 to 10 eggs in sclerophyllous and deciduous habitats, respectively, at similar latitudes on mainland Southern France (Blondel *et al.* 1992a, Blondel & Dias 1994). The Corsican Blue Tits thus could become adapted to the local conditions of sclerophyllous habitat (Blondel *et al.* 1990, 1993; Lambrechts & Dias 1993; Blondel & Dias 1994; Dias 1994).

A consequence of the late breeding season and the southerly latitude of Corsica is a substantially higher mean ambient temperature during chick rearing (20.9°C) than tits experience elsewhere, for example in mainland Southern France (11.5°C; Blondel 1985). It has been proposed that these climatic conditions impose physiological constraints on brood size (Blondel 1991; Blondel & Dias 1994). High temperatures might be particularly critical to nestlings because of their inability to escape high temperatures by seeking more favourable microhabitats (Baldwin & Kendeigh 1932; Mertens 1977). To avoid hyperthermia nestlings must dissipate excess heat by evaporative cooling. The proportion of metabolic heat that nestlings can maximally dissipate by evaporative cooling without risk of dehydration depends on the water content of the food brought by the parents (Mertens 1977). However, the average water content of the nestling diet on Corsica is supposed to be reduced due to a lower proportion of water-rich caterpillars in the diet (Blondel *et al.* 1991). Water may thus be in short supply.

To understand the impact of high temperature and a limited water supply on the breeding biology of Blue Tits we need to investigate the basic physiological response of the birds to these environmental conditions. Since Corsican Blue Tits show local adaptations in some life-history traits (Blondel *et al.* 1990, 1993; Lambrechts & Dias 1993), we might also expect physiological adaptations. For environments characterised by high temperatures and low water supply Dawson (1982) predicts reduced metabolism in order to produce less heat that otherwise has to be dissipated through evaporative cooling. Thus a low metabolism in such environments may contribute to water economisation. We therefore measured metabolic rate and evaporative water loss in full-grown nestlings over a range of temperatures and humidities typically encountered on Corsica. We then compared our estimates with those found in the literature or predicted by allometric equations.

METHODS

Blue Tit nestlings from nestboxes in a small forest plot dominated by alder *Alnus glutinosa* near Galeria (Corsica, 42°25'N, 08°40'E), about 10 km from the main study site, were measured in the laboratory. These birds bred only a few days earlier than those in nearby sclerophyllous habitat (Lambrechts & Dias 1993). Nestboxes were checked at regular intervals, thus age of nestlings were known through their hatching date. Broods were weighed at each visit with a Pesola spring balance to the nearest 0.1 g at several ages to obtain information on their growth. Laboratory measurements were restricted to nestlings 10-17 days old when their weights were already close to the fledging weight. To check whether Corsican Blue Tit chicks at these ages were indeed homeothermic, we made observations on the female's brooding behaviour (Morton & Carey 1971) at the nearby main study site (Pirio; 42°23'N, 08°45'E). Twenty nests were observed for ca. one hour each and the total duration the female spent more than 1 min per visit in the nestbox was recorded. Ambient temperature during the observation was recorded to the nearest 0.5°C with a continuously recording thermometer (Richard, Paris) situated in the centre of the study plot.

Oxygen consumption and evaporative water loss of full-grown nestlings were measured in an open-flow system (Gessaman 1987; Fig. 1). Nest-

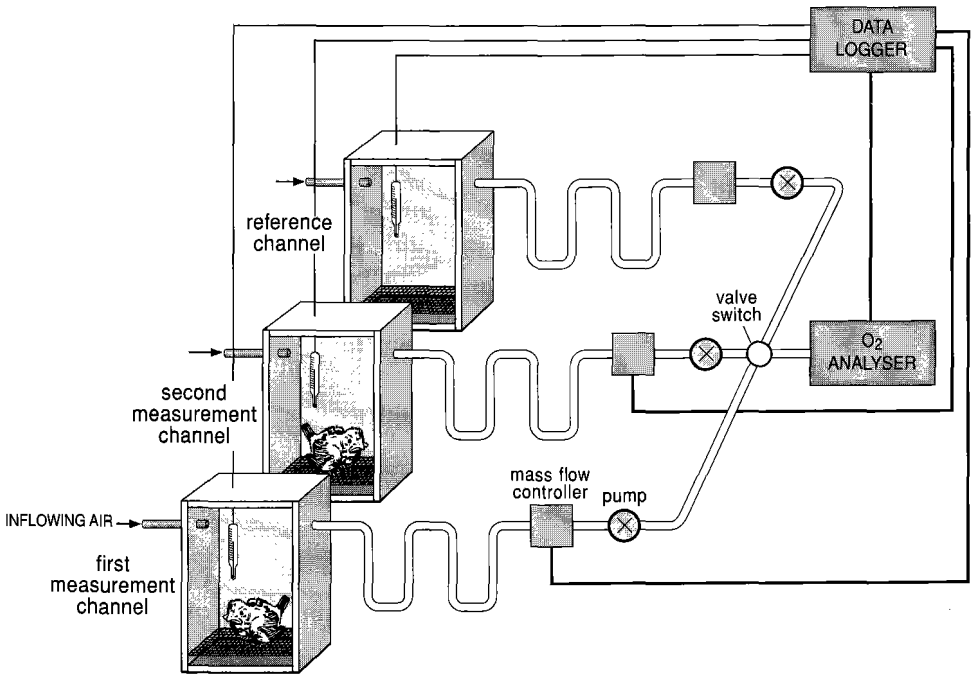

Fig. 1. Schematic representation of the open-flow respirometry system used in this study (see text for details).

lings were taken from their nestboxes in the late afternoon to assure that the young would have sufficient reserves to survive the absence of 2-3 h from their nest. During transport to the laboratory nestlings were kept warm and in the dark. Ca. 1 h after removal from their nest, young were put singly into respirometry chambers. In the respirometry chamber we tried to simulate climatic conditions similar to those we measured in occupied Blue Tit nestboxes in that year. The temperature inside nestboxes averaged ca. 25°C, but were sometimes as high as 30°C. In very hot years temperatures can be even higher (P. Perret pers. comm.). Observed relative humidity in nestboxes during the warmest part of the day ranged between 45% and 75%, corresponding to a range from 10 to 23 mbar of water vapour pressure (maximum = 35 mbar). The temperature inside the respirometry chamber was measured with a thermistor (NTC) and was held more or less constant. During some measurements we raised the temperature up to 35.5°C using warm packs (Grabber), wrapping them outside the chamber. Humidity was checked with a Rotronic meteorological probe (model MP100) humidity sensor which was repeatedly calibrated using salt solutions producing known humidities. In some of the measurements we directed the incoming air over wet cotton to increase the humidity in the respirometry chamber. Water vapour pressure inside the respirometry chamber during the measurements ranged from 12 to 39 mbar. There were 3 respirometry chambers with a volume of ca. 0.8 L each after reduction with foamplastic, containing a platform of wire mesh over a layer of paraffin oil. The oil received droppings produced during the measurement and prevented them to add to the water vapour. The birds were weighed on a electronic balance (Mettler) to the nearest 0.01g before and after the tests and the mean of these two values was taken as their body weight. We always measured two birds at the same time whereas the third chamber remained empty and served as a reference. Ambient air was drawn th-

rough the respirometry chamber at a flow rate of 15 L h^{-1} (measured by mass flow controllers; Brooks Instruments, Veenendaal, The Netherlands, Model 5850E, except in the reference channel where flow rate was controlled at a similar level by a ball flow meter). Outflowing air was passed over a water absorbent (3Å molecular sieve, Merck). Evaporative water loss (EWL, mg H_2O h^{-1}) was determined gravimetrically by the weight gain of the drying tubes. Since the incoming air was not dry, the water absorbed in the reference dryer, corrected for differences in air flow rate, had to be subtracted. From EWL we then calculated the heat dissipated through evaporation (evaporative heat loss, H_e), assuming a heat equivalent of water of 2.26 kJ g^{-1} H_2O. Dried air of the two chambers containing the birds were then directed alternately to the oxygen analyser (AMETEK Applied Electrochemistry model S-3A, Pittsburgh, PA, USA), which measured the difference in O_2-concentration between reference channel (initially set to 0) and measurement channel (dO_2). Only measurements where O_2-concentration returned to 0 when the bird had been removed from the respirometry chamber were retained. Oxygen concentration ($[O_2]$), as well as temperature and flow rate were recorded every 10 s on a data logger (Squirrel 1200, Grant Instruments, Cambridge, UK). Oxygen consumption (Vo_2) was calculated over the last 15 min of the test when O_2-concentrations reached stable levels (on average 67 min after the start of measurement) from equation 4b in Withers (1977):

$$Vo_2 = \frac{[O_2]-([O_2]+dO_2)}{(1-[O_2]+RQ*[O_2])} * \text{flowrate}$$

assuming $[O_2]$ of the ambient air= 20.9% and RQ= 0.8. The metabolic rate (in Watt, W) was estimated from the amount of oxygen consumed, assuming an energetic equivalent of 20 kJ L^{-1} O_2 (Gessaman 1987). Twenty measurements on 13 chicks from 4 different broods were made in the period of 7-17 June 1994. Due to technical failures in 4 of these measurements evaporative water loss could not be accurately estimated and were thus excluded from the analysis of evaporative water loss. Activity of the chicks in the respirometry chamber was regularly checked through a window in the respirometry chamber and noted.

RESULTS

In 1994, Blue Tit nestlings in our study population near Galeria reached an average (± SE) fledging weight of 9.24 ± 0.19 g and a mean tarsus length of 15.83 ± 0.124 mm at day 15 (means of 9, and 6 broods, respectively). After the age of 10 days, the young hardly gained any more weight (Fig. 2). The weight of the full-grown chicks was not different from the weight recorded for a sample of 8 breeding birds at this site and year (9.16 ± 0.118 g; t= 0.26, n.s.). In 5 control broods with at least 1 fledgling, 71% of the hatchlings fledged. Of the unsuccessful young, 40% were found dead in the nest, presumably starved, and the remaining 60% disappeared shortly before fledging for unknown reasons.

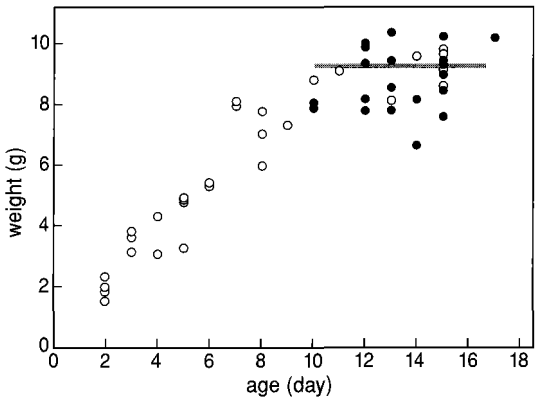

Fig. 2. Body weight of nestling Blue Tits of the study population in relation to age. Figures are mean values per brood (each brood was measured at 2-3 different ages). Filled symbols represent the mean chick weight of broods from which chicks were taken for respirometry measurements. The horizontal dashed line indicates the mean fledging weight (= 9.24 g) which is very close to the mean breeding weight of adults (9.16 g).

Table 1. Twenty nests have been observed during one hour and the total duration females spent in the nestbox, presumably brooding the young, was noted. Excluded are visits shorter than one min. Figures given in the table are the proportion of time the young had been brooded (median and range, n= sample size), depending on the age of the brood (1st week= 4-7 days, 2nd week 8-15 days, day 0= day of hatching) and the ambient temperature. Younger chicks were brooded for a larger proportion of the time at all temperatures (Mann-Whitney U test, Z= -3.39, P< 0.001). Chicks were brooded for a longer time at temperatures below 20°C than at temperatures above 20°C in their first week (Z= -2.20, P< 0.05), but not any more in their second week (Z= -1.22, n.s.).

	1st week	2nd week
All	21.7%	0%
	(0-35%)	(0-3.3%)
	n= 9	n= 11
Temperature <20°C	29.4%	1.7%
	(21.7-35%)	(0-3.3%)
	n= 4	n= 4
Temperature >20°C	10.0%	0%
	(0-28.3%)	(0-3.3%)
	n= 5	n= 7

The female's attentiveness on the nest decreased with the age of the young (Table 1). During daylight hours, females spent on average 13 min h^{-1} (21.7%) brooding chicks of 7 days and younger, but hardly no brooding was observed at nests with older chicks (Table 1, Z = -3.39, P< 0.001). Furthermore, during the first nestling week females spent more time brooding at ambient temperatures below 20°C (29.4%) than at temperatures above 20°C (10%, Table 1, Z = -2.20, P< 0.05). This means that after the first week, Corsican Blue Tit nestlings can be considered as homeothermic (Morton & Carey 1971).

Metabolic rate increased with decreasing temperature and increased with body weight (Table 2). The effect of temperature on metabolic rate was also evident within 6 individuals tested at different days on different temperatures (analysis of covariance; temperature (covariable): $F_{1,6}$= 10.78, P< 0.05, estimate of the slope -0.036 ± 0.0102 W $°C^{-1}$; individual (intercept): $F_{5,6}$= 3.78, P= 0.07; the interaction term was not significant). There were differences in metabolic rate among individuals although statistically not significant (P= 0.07), but heavier individuals had higher estimated intercepts (Spearman rank correlation test, R_s= 0.94, n= 6, P< 0.05). Above 30°C mass-specific metabolic rate did not change anymore with temperature, but increased with decreasing temperature at temperatures below 30°C (Fig. 3).

Evaporative water loss (EWL) increased nonlinearly with temperature (Fig. 4). EWL averaged 7.04 mg $H_2O\ h^{-1} \cdot 9^{-1}$ at temperatures below 30°C, but increased significantly at higher temperatures ($F_{1,5}$= 8.87, P< 0.05, R^2= 0.57). The ratio between the heat lost through evaporation (evaporative heat loss, H_e, see methods) and the heat produced by the metabolism (H_m) gives an idea of the contribution of evaporation to the thermoregulation

Table 2. Multiple regression of metabolic rate (√-transformed to obtain normal distribution in the residuals, n= 20) on temperature, body weight and humidity as independent variables. Neither chick age nor whether they were active in the respirometry chamber or not had a significant effect on metabolic rate and are not included in the present model. Metabolic rate increased with increasing body weight, and decreased with increasing temperature ($F_{2,17}$= 14.23, P< 0.001, R^2= 0.58). The water vapour pressure had no significant effect on metabolic rate.

Factors	t	P<	estimate	±	SE
Temperature	-4.85	0.001	-0.018	±	0.0037
Body weight	2.22	0.05	0.032	±	0.0143
Water vapour pressure	0.55		-		
Constant	3.96	0.001	0.659	±	0.1666

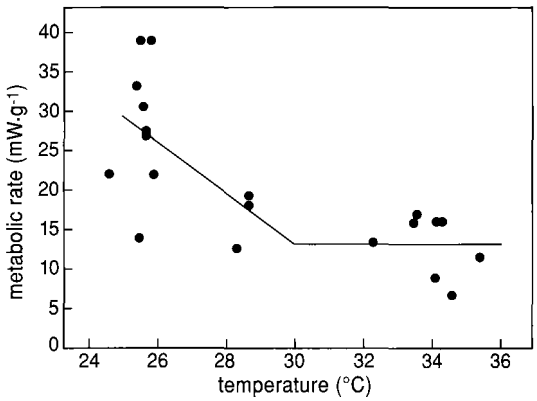

Fig. 3. Mass-specific metabolic rate in relation to temperature. The combined regression model with a threshold at 30°C (indicated by the line, see text) explains a slightly larger fraction of variation in mass-specific metabolic rate (53.5%) than a linear model (line not shown, 50.7%).

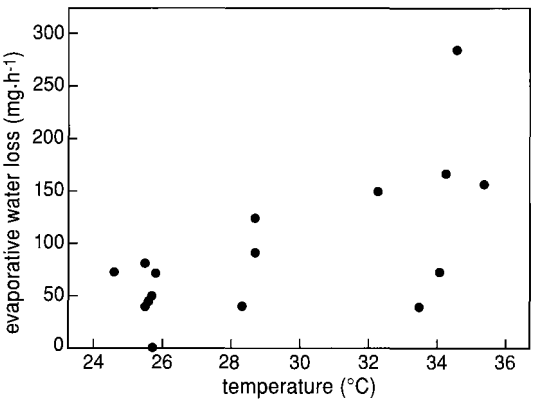

Fig. 4. Evaporative water loss (EWL) in relation to temperature. EWL increased non-linearly with increasing temperature ($F_{1,14}$= 10.45, P< 0.01; EWL= 0.189*(temperature)^2 - 71.85, R^2= 0.39). Neither body weight (t= 1.61, n.s.) nor water vapour pressure (t= 0.18, n.s.) influenced EWL.

of an organism (Calder & King 1974). For Corsican Blue Tit nestlings the proportion of the metabolically produced heat that was dissipated by evaporative cooling increased with ambient temperature (temp):

$$(H_e/H_m)= 0.0006 * e^{0.219*temp}$$

($F_{1,14}$= 11.15, P< 0.01, R^2= 0.44). That means that at 25°C 14.3% of the metabolic heat was dissipated by evaporative cooling and at 30°C 44.2%. We calculated dry conductance (C_{dry}, in mW g^{-1} °C^{-1}) following the approach of McNab (1980):

$$C_{dry}= (H_m-H_e)/(T_b-T_a)$$

where we assumed T_b= 40°C for Blue Tit chicks (O'Connor 1975), and T_a= ambient temperature. C_{dry} decreased with increasing ambient temperature (C_{dry}= 6.10 - 0.18 * T_a; $F_{1,14}$= 8.54, P< 0.05, R^2= 0.33).

DISCUSSION

We limited our measurements to nestlings which were at least 10 days old. The percentage of time the young in their second week were brooded was low and independent of weather, indicating that these nestlings are homeothermic (Morton & Carey 1971) over the temperature range used in our measurements. This has also been found in other Paridae (Odum 1941; Brewer 1961; Deckert 1964). Breeding weight of Blue Tits on Corsica is 15% lower (Blondel *et al.* 1992b) than continental Blue Tits (10.9 g Dias 1994). This is very similar to the weight of breeding adults reported here (9.2 g) and to the weight of the nestlings used in our measurements (Fig. 2). Starvation of chicks in the nest seemed to be rare (12%). Thus, the nestlings in our measurements were more or less full-grown, homeothermic, and in good condition.

Heavier, and presumably larger birds, had a higher metabolic rate. Although body weight may not be an ideal predictor of metabolic rate, since it also includes metabolically inactive components (e.g. fat and water), it yielded qualitatively the same results as taking tarsus length as a measure of body size (analysis not shown), and it allows direct comparison with allometric predictions from the literature. However, developing birds might have a very variable content of metaboli-

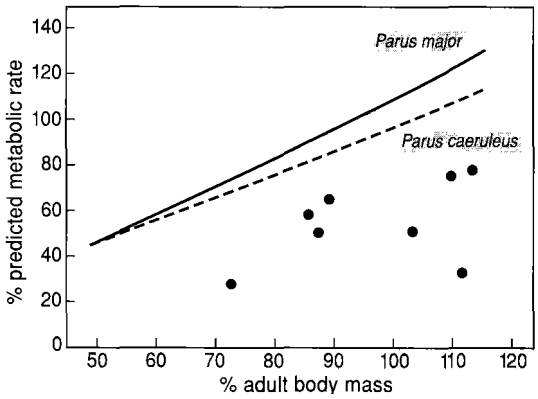

Fig. 5. Comparison of BMR in relation to body mass for 3 tit populations. To compare among nestlings of different body mass all values are expressed as percentages of adult values. (1) Solid line represent Great Tit nestlings from a Dutch population (Mertens 1977, adult body mass= 17.7 g after Tinbergen & Dietz 1994, predicted adult BMR= 0.296 W). (2) Interrupted line represents Blue Tit nestlings from an English population (after O'Connor 1975, adult body mass= 11.3 g, predicted adult BMR= 0.214 W). (3) Closed symbols represent measurements of Blue Tit nestlings from Corsica (this study, adult body mass= 9.16 g, predicted adult BMR= 0.215 W). BMR for adults were predicted after Aschoff & Pohl (1970) for summer acclimatised birds in the inactive phase of the daily cycle for (1) and (2); for summer acclimatised birds in the active phase of the daily cycle for (3).

cally inactive tissue due to individual variation in tissue maturation and this might lead to the observed high variance in mass-specific metabolic rate (see also data in O'Connor 1975). The metabolic rate decreased with increasing temperature between 25 and 30°C, and remained constant above 30°C. The thermoneutral zone must therefore extend from ca. 30°C to at least 35°C. The metabolic rate above 30°C may then estimate basal metabolic rate (BMR) and was measured as 0.117 ± 0.014 W per bird at an average weight of 8.83 g. This value might be a small overestimation of BMR since some birds were probably not yet truly postabsorptive and heat increment of feeding might had added to the metabolism, depending on the time since last feeding and the meal size. Furthermore, all young were still growing feathers to a variable degree. All of these factors might also contribute to a larger variation in measurements.

Table 3. Observed and predicted (for adult passerine birds) physiological parameters for full-grown Corsican Blue Tit nestlings.

	Observed	Predicted
Evaporative water loss [g H_2O day^{-1}]	1.48	2.50[a]
H_e/H_m at 25°C [%]	14.3	13.8[b]
H_e/H_m at 30°C [%]	41.2	25.1[b]
Thermal conductance [mW g^{-1} $°C^{-1}$]	1.432	1.745[c]
Lower critical temperature [°C]	30[d]	26.4[e]

[a] Calculated from the relation g H_2O day^{-1}= $1.56m^{0.217}$ from Crawford & Lasiewski (1968); expected value at 25°C (m= body weight= 8.83g).
[b] Calculated from the relation %= $5+1.48e^{0.087T}$ from Calder & King (1974) (T= ambient temperature).
[c] Calculated from the relation mW g^{-1} $°C^{-1}$= $4.784m^{-0.463}$ for α measurements from Aschoff (1981).
[d] minimal estimate (see text).
[e] Calculated from the relation °C= T_b-$9.46m^{0.167}$ (assuming that T_b= 40°C) from Weathers & van Riper (1982) (T_b= body temperature).

How does the estimate of BMR of Corsican Blue Tit nestlings compare to other bird species? If there is an adaptation to a warm climate a lower BMR has been predicted (Dawson 1982). A common basis for comparisons are allometric equations which relate metabolic rate to body weight (e.g. Aschoff & Pohl 1970). The estimate of BMR for the Corsican nestlings is only 61.6% of the predicted value for adult tits in the active phase of their daily cycle (0.190 W for a bird of 8.83 g). However, there are only few measurements on BMRs on altricial birds in the nestling stage. Fortunately, there are two sets of measurements on BMR for nestlings of different ages in Paridae from more northerly continental populations: Blue Tits from England (O'Connor 1975) and Great Tits *Parus major* from the Netherlands (Mertens 1977). Mertens (1977) has shown that in Great Tit nestlings BMR scales differently on

Table 4. Daily weight increment during the linear phase of nestling growth (between 5 and 10 days of age) in different Blue Tit populations. Observed growth rates were based on unpublished data unless otherwise stated.

Study area	Latitude	Growth rate ($g\ day^{-1}$)	Reference
Wytham, Oxfordshire, GB	51°78'N	1.029	O'Connor 1975
		0.940	Gibb 1950
Oberrheinebene, South Germany	48°16'N	1.002	Neub 1977
Blauen, NW-Switzerland	47°29'N	0.895	R.G. Nager
Rouvière, Southern France	43°64'N	0.992	J. Blondel & R. Julliard
Galeria, Corsica	42°25'N	0.836	this study
Pirio, Corsica	42°23'N	0.770	J. Blondel & S. Hurtrez-Boussès

body mass than predicted from interspecific relationships based on adult birds (slope 1.278). Very similar slopes of nestling's BMR on body mass exist also in House Wrens *Troglodytes aedon* (Kendeigh 1939 in Mertens 1977) and Blue Tits from England (data extracted from O'Connor 1975, slope= 1.109 ± 0.219). To compare BMR measurements among nestlings of different populations of tits with different body weights we expressed the intraspecific relationship between nestling's weight and their BMR as percentages of the values of adults (Fig. 5). Observed values of relative BMR for the Corsican Blue Tit population were significantly lower than the predicted values, corrected for differences in body weight, of Great Tits (t_7= -7.04, P< 0.001) and Blue Tits from England (t_7= -6.08, P< 0.001).

Lower BMR had been observed in several species of tropical birds compared to species from temperate zones (Weathers 1979; Bryant & Hails 1983; Hails 1983). Within-species differences in BMR in relation to thermal environment had also been reported in the literature (Hudson & Kimzey 1966; Trost 1972; Arad & Marder 1982; Kersten & Piersma 1987). Lower metabolic rate of Corsican Blue Tits might be the result of poor feeding of the parents to the young (Ketterson & King 1977; Shapiro & Weathers 1981). However, in the study population conditions of fledglings seemed to be good judged from their body weight relative to adult's breeding weight and from the low mortality due to starvation. Thus poor feeding conditions is an unlikely explanation for the observed reduction in metabolism. Alternatively low BMR could represent an adaptation to economise water (Dawson 1982). A consequence of this reduction in metabolic rate will be that at high ambient temperatures less metabolic heat has to be dissipated through evaporative cooling. The observed reduction in metabolism would result in an expected saving of water of 38.5%. In the present study at 25°C Blue Tit nestlings lost 40.8% less water than predicted from an allometric relationship (Table 3), which is very close to the expected value.

Physiological adaptations to a warm climate manifest themselves not only through a reduction in metabolic heat production (H_m), but through other thermoregulatory parameters as well, such as dry conductance (C_{dry}) and lower critical temperatures (T_{LC}) (Calder & King 1974). These parameters can be related to each other through the Scholander model (Calder & King 1974):

$$H_m = C_{dry}(T_b - T_{LC})$$

If body temperature (T_b) is to remain constant we would expect a reduction in dry conductance (C_{dry}), or an increase in T_{LC}, or both, when H_m is reduced. We indeed found a reduction of 17.9% in C_{dry} compared to the allometric expectation (Table 3) under the assumption of constant body temperature of 40°C. From the model in Fig. 3 T_{LC} must be at least 30°C. The linear regression model (Table 2) intersects with the estimated BMR

at 34°C. T_{LC} is thus supposed to be between 30 and 34°C. This range is higher than the value predicted for a bird of the same weight (Table 3). A consequence of increased T_{LC} might again be a reduction in water expenses. Evaporative water loss increases steeply only above T_{LC} (Dawson 1982), but temperatures in the nestboxes were rarely above T_{LC}. If T_{LC} would have been around the predicted value chicks would much more frequently encounter conditions where water expenses are high.

It had been suggested that maybe as a consequence of reduced metabolic rate tropical birds grow more slowly than do temperate zone birds (Ricklefs 1976). Growth pattern can vary considerable within bird species and might be based partly on genetic differences (Starck *et al.* 1995). It might be thus expected that Blue Tits on Corsica encountering higher temperatures and showing reduced BMR grow more slowly than continental Blue Tits in more temperate zone climate. As Table 4 shows Blue Tits on Corsica had indeed a lower growth rate than reported for any other European Blue Tit population.

Thus the low BMR allows Blue Tit nestlings important savings in their water expenses by (i) reducing the heat production which has to be dissipated and (ii) shifting the zone of high costs of evaporative cooling towards such high temperatures that nestlings hardly never meet them. However due to a lower metabolism they will suffer from a reduced capacity to produce heat which might result in a higher susceptibility to cool temperatures during rainy periods. A low metabolism might also result in a reduced growth rate of chicks on Corsica.

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SAMENVATTING

Pimpelmezen *Parus caeruleus ogliastrae* op Corsica broeden later in het seizoen dan de mezen van het Europese continent. Deze aanpassing aan de late voedselpiek aldaar maakt dat de temperatuur tijdens het broedseizoen hoog is. Door deze hoge temperaturen verdampen de jongen veel water, terwijl het watergehalte van de aangevoerde prooien laag is. Als water een limiterende faktor is verwachten we fysiologische aanpassingen van de jonge Pimpelmezen aan het warme klimaat, zoals een verlaagd metabolisme. Wij hebben het rustmetabolisme en het waterverbruik van 20 volgroeide nestjongen van Corsicaanse Pimpelmezen gemeten met behulp van een 'open-flow' respirometer. Het rustmetabolisme bij thermoneutrale temperaturen is slechts 0.117 W, hetgeen aanzienlijk lager is dan verwacht op basis van allometrische relaties. De verdampingssnelheid bij 25°C lag 40.8% onder de waarde verwacht op basis van het lichaamsgewicht. De gevonden besparing van verdampingswater komt overeen met de verwachte besparing als gevolg van de verlaagde metabolische warmteproduktie. De fysiologie van nestjonge Pimpelmezen op Corsica lijkt hierdoor meer op die van soorten van een heet en droog klimaat dan op die van continentale Europese Paridae.

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